

XV. Mimetic Forms of *Papilio dardanus* (*merope*) and *Acræa johnstoni*. By EDWARD B. POULTON, D. Sc., M.A., Oxon., Hon. LL.D., Princeton, F.R.S., Hope Professor of Zoology in the University of Oxford, Fellow of Jesus College, Oxford.

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PLATES XVII-XXII.

A. MIMETIC FORMS OF *Papilio Dardanus*, BROWN.

I. *Synepigonic Group bred in 1904 by G. F. Leigh, F.E.S., from a trophonius ♀ form of P. dardanus subspecies cenea, near Durban.*

This piece of work is an interesting and important addition to the breeding experiments upon *P. dardanus* undertaken by Mr. Leigh in 1902 and 1903. (Trans. Ent. Soc., Lond. 1904, p. 677.) As a result of this latest inquiry the *trophonius* ♀ form has for the first time been bred from a parent of the same form.

On May 4, 1904, Mr. G. F. Leigh observed a *trophonius* female laying eggs on the food-plant, at Bellair, five miles from Durban, Natal. He collected the eggs but the parent butterfly escaped. From these eggs Mr. Leigh succeeded in breeding six males and seven females. Of these all the males and five of the females are represented about two-fifths of the natural size on Plate XVII, Figs. 1-11. The dates of emergence are given in the explanation of Plate XVII (pp. 312, 313), so it is not necessary to repeat them here. The two unfigured females were in both cases *cenea* forms:—one greatly deformed and shrivelled (pupated June 30, 1904, emerged July 30: the ninth to emerge); one not included in Mr. Leigh's consignment (it was the twelfth to emerge).

(a) *The males.*

The six males of this interesting synepigonic series are represented on Plate XVII, Figs. 1-6. If compared with TRANS. ENT. SOC. LOND. 1906.—PART II. (SEPT.)

the account (in Trans. Ent. Soc. Lond. 1904, p. 684) of the equal number of males in the family bred in 1902 by Mr. G. F. Leigh, it will be seen that the latter possess as a whole far darker submarginal bands on the hind-wing. A single male (Plate XVII, Fig. 6) and that by far the darkest of the 1904 family is about as dark as one of the medium specimens of 1902. The other five are far less dark than any except the dwarfed "*specimen 6*." It is not necessary to describe and compare the condition of the submarginal bands, inasmuch as the whole series is figured, and this is a character which can be reproduced with great fidelity, and can be as well compared in somewhat reduced figures as in those which represent the natural size.

The hind-wings of these males, less heavily marked as compared with the 1902 and 1903 groups, probably exhibit seasonal differences, and the same explanation is even more certain for the under-side coloration, which is darker and more uniform in the specimens here described.

It will be noticed that the inner border of the black margin of the fore-wing is strongly serrated in Fig. 5, less so in Figs. 4 and 6. This serration is characteristic of both male and female in the ancestral *Papilio meriones* of Madagascar, but strangely enough it does not reappear in the most ancestral of the continental males which I have had the opportunity of examining. I do not find it in *P. antinorii* (3 males), *P. polytrophus* (5 males), or in *P. merope* from the west coast. It appears however in a small proportion of the males from the northern end of the Victoria Nyanza and in the southern and eastern *cenea*. In the latter case it is to be found not uncommonly among the captured specimens as well as among those that have been bred. It is certainly remarkable that this ancestral feature should on the continental area be chiefly found in the most highly specialized of all the sub-species,—*cenea* of the south and south-east.

(β) *The females.*

The *trophonius* offspring (Plate XVII, Fig. 7) is seen to be a perfectly normal example of the southern type. As regards the *cenea* forms, the relative development of buff and white in the spots of the fore-wings may be shown by comparison with the earlier family classified on p. 681 of Trans. Ent. Soc. Lond. 1904.

Plate XVII, Fig. 8, about the same as No. III on p. 681.

"	"	"	9	}	"	"	"	"	Nos. IV-V	"	"
"	"	"	10								
"	"	"	11								
The unfigured cripple				}	"	"	"	"	"	I-II	"

The two *cenea* represented in Figs. 8 and 11, on Plate XVII, show the influence of *trophonius* parentage (see description of Figures, p. 313).

In the latter pages of this memoir these 11 specimens, both male and female, will be often referred to and compared with other forms.

II. *Papilio dardanus* ♀ f. *trimeni*, new form.

In his Presidential Address to the Entomological Society of London in 1898 (Proc. 1897, pp. lxxxviii, lxxxix) Mr. Roland Trimen, F.R.S., described a remarkable form of the female *dardanus*, sub-species *tibullus*, from Zanzibar, in the Hope Department. After expressing the opinion that the West African *dionysos* was the least modified as compared with the male of all the various tail-less continental female forms known until that time,* he went on to describe the specimen from Zanzibar as "a much closer approximation to the masculine coloration. In this female the transverse trace of black in the fore-wings is even fainter than in the *dionysos* form, and the colour of the wide pale spaces and the hind-marginal spots in all the wings is almost exactly of the pale creamy-yellowish tint of the male *P. cenea*; and on the under-side, while the pale yellowish of the fore-wings is better divided by blackish than on the upper-side, the colouring of the hind-wings corresponds much more nearly to that of the male than in any other female I have seen—the characteristic break in the submarginal brownish band being moreover very complete and wide. There can be no doubt that in this specimen we have a marked case of reversion to the original colouring of the female, but it is unaccompanied by any inclination towards the recovery of the lost tail of the hind-wings." In the same address (p. lxxxviii) the distinguished African naturalist expresses the opinion that "we may not unreasonably hope to dis-

* Speaking of *dionysos*, Mr. Trimen quotes his earlier paper in Trans. Ent. Soc. Lond. 1874. The reference is erroneously given as p. 178: it should be p. 148.

cover, at some point in the wide territories between Abyssinia and Zanzibar, females of the *Merope*-group exhibiting stages intermediate between the long-tailed mimetic females of *P. antinorii* and the entirely tail-less ones of *P. cenca*."

It was reasonable not to attempt to name this primitive variety while it remained as a single example; but now that it has been discovered in large numbers as one of the female forms of the sub-species *polytrophus*, Jordan, on the Kikuyu Escarpment, the case is different. It is one of the most instructive if not actually the most instructive of all the female forms of *dardanus*; and I propose to call it *trimeni*, in honour of the great naturalist who solved the mystery, and laid a firm foundation for all future work upon the most interesting and complex example of mimicry as yet known throughout the world.*

The specimen referred to by Mr. Trimen is here represented on a slightly reduced scale on Plate XIX, Fig. 1. In Plate XVIII, Fig. 1, one of the smaller *trimeni* forms from the Kikuyu Escarpment is represented of about the natural size. Of these there are four in the Hope Department. Judging from these four specimens the ground colour is sometimes yellow, exactly like that of the male (1), sometimes of a rather paler shade (2), and sometimes a little darker (1).

(a) *Occasional occurrence of rudimentary "tails" to the hind-wing of trimeni and hippocoon.*

The *trimeni* form frequently possesses ancestral characters additional to those described in the Presidential Address. The most interesting of these supplies the confirmation of Mr. Trimen's prediction that stages would be found "intermediate between the long-tailed mimetic females of *P. antinorii* and the entirely tail-less ones of *P. cenca*." The specimen represented on Plate XVIII, Fig. 1, is seen to have a small but distinct rudimentary "tail," containing an extension of the third median nervule. This nervule also enters the tail in the male, showing that the rudimentary tail of the female is entirely homologous with that of the other sex. The other three specimens of *polytrophus* ♀ f. *trimeni* do not exhibit this feature, but it is

* It is perhaps unnecessary to say that I allude to the great monograph in Trans. Linn. Soc., vol. xxvi, 1870, Pt. III, 1869, p. 497.

possessed by an interesting example, to be described below (see p. 290), showing the origin of *trophonius* from *trimeni*. It is also possessed by two examples of the sub-species *merope* ♀ f. *hippocoon* in the National Collection. These specimens, both from the west coast, are represented in Plate XIX, Figs. 2 and 3.

(β) *Prominence of submarginal pale spots in hind-wing of trimeni, etc.*

Another primitive feature usually characteristic of *trimeni* is the large size and prominence of the submarginal pale spots in the black border of the hind-wing. These spots are of course persistent traces of the yellow ground colour of the male and unmodified female enclosed between the two black bands parallel with the hind-margin of the hind-wing. The band of ground colour is widest and most prominent between the root of the "tail" and the "inner gap," as will be seen by a glance at Figs. 1-6 on Plate XVII. Furthermore this especially prominent patch is widest immediately on the inner side of the root of the "tail," because it is here continuous with the ground colour in the "inner gap" (Plate XVII, Figs. 1-5) or enters the bay by which the closed gap is indicated (Fig. 6). It is precisely in this region, between the second and third median nervules, that the pair of submarginal spots even in the most specialized female forms often tend to be largest and most conspicuous. This is well seen in the *cenea* forms represented on Plate XVII, Figs. 8 and 11; and in the *hippocoon* shown on Plate XIX, Figs. 2 and 3. In the more primitive *trimeni* we expect to find and we do find these tendencies more marked and accompanied by a far higher degree of development of the whole series of paired submarginal spots on the hind-wing. The special size of the pair marking the position of the inner gap is well seen in the *tibullus trimeni* represented on Plate XIX, Fig. 1, and even better in the *polytrophus trimeni* of Plate XVIII, Fig. 1. In this latter the two enlarged spots have fused into a single and prominent patch. The development of the series of submarginal spots in *trimeni* is however far better seen in three specimens of this form of the sub-species *polytrophus* in the Hope Department,—specimens which in other respects were less instructive than that represented on Plate XVIII, Fig. 1.

We can at once understand by the study of the examples

of *trimeni* figured on Plate XVIII, Fig. 1, and XIX, Fig. 1, and by comparison with the *hippocoon* forms on the same plates (XVIII 2, XIX 2-3), why it is that the submarginal yellow ground colour should be represented in the mimetic females by a pair of pale spots between each pair of nervules. It is evidently because the marginal development of black was brought about not only by a growth in width of the two marginal black bands of the male (Plate XVII, Figs. 1-6), but was also aided to an important extent by the appearance of black inter-nervular streaks. These naturally cut the ground colour still persisting between each pair of nervules into two halves.

(γ) *Traces of costal and inner gaps in black margin of hind-wing of trimeni, etc.*

Apart from the indication of the "inner gap" afforded by the special development of the corresponding pair of pale submarginal spots, other distinct traces of both gaps are among the primitive features of *trimeni*. They are especially strongly developed in the specimen shown in Plate XVIII, Fig. 1. The "costal gap" is remarkably clear in the figure, while the site of the "inner gap" is rendered visible by two faint yellow streaks passing outwards into the broad black margin. They are better seen in the right hind-wing of Fig. 1. The *trimeni* represented on Plate XIX, Fig. 1, is a ♀ form of the east coast sub-species *tibullus* in which the black band of the male is more developed than elsewhere, while the gaps are reduced to a minimum (Trans. Ent. Soc. Lond. 1904, p. 683). Nevertheless the "costal gap" can be clearly recognized. It is seen in Fig. 1 that the inner border of the black margin is not curved parallel with its outer border forming the edge of the wing but is made up of two straight lines meeting in an obtuse angle. This angle is the point where the central yellow invades the black margin most deeply and represents the costal gap of the male. This identification will be at once admitted when Fig. 1 on Plate XVIII is compared with Fig. 1 on XIX. The squarish shape thus originating persists in many examples of the more specialized female forms. It may be distinctly seen on the two *hippocoon* (Figs. 7, 8) and three of the *cecea* (Figs. 5, 6, 10) forms represented on Plate XXXI of Trans. Ent. Soc. 1904; and in the present memoir in *trophonius* represented on Fig. 7 of Plate XVII, and the

cenea on Fig. 11 of the same Plate. It is remarkably distinct in the *polytrophus* ♀ f. *hippocoon* shown on Plate XVIII, Fig. 2, although barely recognizable in the same forms from the west coast seen in Figs. 2 and 3 of Plate XIX.

III. *Papilio dardanus*, sub-species *merope* ♀ f. *dionysos*,
Doubl.

Before proceeding to consider the origin of the mimetic female forms of *dardanus* it is necessary to say a few words of this remarkable and primitive variety which is not uncommon on the west coast. It is very probable that it also occurs among the wonderful series of *polytrophus* females from the Kikuyu Escarpment, but I have not yet met with an example.

In *dionysos* the hind-wings are those of the *merope* ♀ f. *trophonius* except that they are of a distinctly paler tint and thus nearer to *trimeni*. The costal gap is also very strongly marked. The fore-wings possess the black and white coloration of *hippocoon*, but with a primitive diminution of the black markings which is very like *trimeni*. In fact in one specimen (Cameroons: Cutter: 1869) in the Hope Department the oblique bar dividing the two chief white markings of the fore-wing is even less developed than in any of the five specimens of *trimeni* in the same collection. It is probable that *dionysos* was an early variant from *trimeni*, presenting a mixture of the characters which in other proportions were to be selected into *trophonius* on the one hand and *hippocoon* on the other.

IV. *The sub-species of Papilio dardanus* (= *merope*).

Before discussing the origin of the mimetic female forms it is necessary to consider the division of *dardanus* into sub-species. Dr. Karl Jordan* has examined 509 males and 270 females in the Tring Zoological Museum. Excluding the forms from N.E. Africa and Madagascar and only considering the males Dr. Jordan finds south of Sierra Leone five sub-species distinguished chiefly by the extent of black on the hind-wings. Differences in sex-organs are confined to the valve-edges. Dr. Jordan's five sub-species are as follows:—

* Der Gegensatz zwischen geographischer und nichtgeographischer Variation. Zeitsch. f. wissenschaft. Zool., Bd. lxxxiii. Dr. F. A. Dixey has very kindly lent me for the purpose of this memoir an abstract which he has prepared of this interesting paper.

- (1) *P. cenea*. S. Africa. Transition to next form in geographical position and morphological character is complete.
- (2) *P. tibullus*. Delagoa Bay northwards to Mombasa; west limit unknown, but occurs in Uganda.
- (3) *P. polytrophus*. B. E. Africa.
- (4) Transitional forms from Victoria Nyanza.
- (5) *P. dardanus dardanus*. Unyoro to west coast. Congo specimens are larger, as in some other cases.

Dr. Jordan furthermore states that *P. dardanus* is not sharply marked off into geographical forms. East and west coast examples can be distinguished, but neither assemblage is a complete unit. It is significant that the valve-process is generally present in eastern and absent from western forms.

In the following pages I have followed Dr. Jordan's conclusions and terminology with the single exception that I have called the fifth sub-species *dardanus merope* instead of *dardanus dardanus*.

V. *The origin of the mimetic female forms of Papilio dardanus from the ♀ f. trimeni.*

There can be little doubt that all the well-known mimetic females of *dardanus* as well as the latest discovery *planemoides* originated by modification of this primitive female form, either directly or by the combination and development of characters on their way to produce other forms. I propose to consider the evolution of these forms in the order of specialization, beginning with the most primitive:—

(1) *Hippocoon*. The relationship of *hippocoon* to *trimeni* is at once seen by comparing Fig. 2 with Fig. 1 on Plate XVIII. The transformation is remarkably direct and simple, consisting merely in the greater intensity and sharpness of black markings already distinctly indicated in *trimeni*, and in the alteration of the pale yellow tint of the latter into white. There are four examples of this form from the Escarpment in the Hope Department. The other three are fairly represented by the figure of the fourth on Plate XVIII, Fig. 2, and it is rather surprising that none of them possess an indication of rudimentary "tails." It cannot be doubted however that *hippocoon* is by far

the most primitive of the mimetic female forms of *dardanus*, and I have been deeply interested to find well-marked rudimentary "tails" on two specimens from the west coast. These examples of the sub-species *merope* ♀ f. *hippocoon* exist in the National Collection, the "tails" being pronounced in one (Plate XIX, Fig. 2), distinct in the other (Fig. 3). By kind permission of the authorities I am able to submit the reproductions, referred to above, of Mr. Alfred Robinson's beautiful photograph, made in the Oxford University Museum.

The sporadic occurrence of this ancestral feature in association with precisely that form which still retains the most primitive pattern is a difficulty to be surmounted by those who have been inclined to minimize or even to deny the occasional cropping-up by reversion of long-lost characters.

The name *hippocoonoides* has been given by Haase to this form in the eastern and southern sub-species *tibullus* and *cenæa*. This seems to me a most unnecessarily complex and inconvenient procedure. The *trophonius* of the western sub-species *merope* is at least as different from that of the southern *cenæa* as are the two forms of *hippocoon* from the same areas. It is pretty certain indeed that each female form of every sub-species has certain peculiarities and is not exactly like the same form of any other sub-species. But this is quite sufficiently indicated by prefixing to the female form name the sub-specific name. *Papilio dardanus* sub-species *merope* ♀ f. *hippocoon* of the west coast is naturally different from *P. dardanus* sub-species *cenæa* ♀ f. *hippocoon* from Natal, and it is quite unnecessary to express this by turning the last name into *hippocoonoides*. To do so without making corresponding changes in the other forms is inconsistent; to be consistent in this respect is immensely to increase and to increase uselessly an already tremendous terminology.

The *hippocoon* forms are everywhere mimics of the abundant and conspicuous Danaines, *Amauris niavius* of the west and its sub-species *dominicanus* of the east coast and the south. They also exhibit a strong secondary mimetic approach to their Nymphaline co-mimics *Euralia anthedon* of the west and *E. wahlbergi* of the east and south (Trans. Ent. Soc., Lond., 1902, p. 486). The *hippocoon* form is probably dominant in all the sub-species of *dardanus* except *cenæa* and perhaps *polytrophus*; and it is present in fair proportion in both these.

(2) *Trophonius*. This form possesses the pattern of *hippocoön*, but white has been replaced by fulvous over the great continuous patch occupying most of the hind- and a large part of the fore-wing. The remaining pale markings are white, so that the yellow of *trimeni* in part originated white and in part fulvous,—a more complex change than that which produced *hippocoön*. Considering the identity of pattern I first supposed that *trophonius* arose from *hippocoön* instead of having an independent origin in the *trimeni*. Although the former view may be correct, the latter is I think more probable, being strongly supported by an interesting specimen from the Kikuyu Escarpment, in the Hope Department. In this butterfly the great patch is fulvous except upon the distal border of the part upon the fore-wing. This border, together with all the other pale markings on both wings, is not white like *hippocoön*, but retains the yellow of *trimeni*. The specimen furthermore possesses a rudimentary “tail” nearly as much developed as that of the *trimeni* represented on Plate XVIII, Fig. 1, while the sub-marginal yellow spots of the hind-wing are very large and prominent, far more so than in the particular specimen of *trimeni* just referred to. This specimen, with its primitive features, strongly supports the direct independent origin of *trophonius* from *trimeni*, the most convincing evidence being supplied by the pale markings which had not been converted into white, but remained of the ancestral yellow.

The *trophonius* form at any rate of the *merope* sub-species appears to be more unstable and is probably a more recent development than either of the other mimetic female forms *hippocoön* and *plunemoides*. A specimen in the Hope Department (Angola: Rogers: 1873) presents a very primitive form of the oblique black bar dividing the two chief pale spaces of the fore-wing. It is even less developed than in a specimen of *dionysos* in the same collection and much like that of the *tibullus trimeni* represented on Plate XIX, Fig. 1. *Merope trophonius* is very apt to appear as a variety in which the fulvous tint overspreads the whole of the pale markings of both wings. One of the two *polytrophus trophonius* forms at Oxford is of this variety. It is moreover a very poor mimic of *Limnas chrysippus* as compared with the smaller more deeply-coloured *trophonius* of the *cenea* sub-species (Plate XVII, Fig. 7). It is also noteworthy that the *merope trophonius*

does not, so far as I am aware, present a variety with white hind-wings like the forms of *Limnas chrysippus*, var. *alcippus*, universal on the west coast.

Trophonius forms, although probably always relatively rare, occur in all five sub-species distinguished by Dr. Jordan.

(3) *Cenea*. Here too it is almost certain that the female form developed direct from *trimeni*, the ancestral yellow ground colour being transformed into buff without first becoming white. The evidence is similar to that advanced in the case of the last female form, but is stronger, inasmuch as there is not in *cenea* that close resemblance to the pattern of *hippocoön* which is borne by *trophonius*. Comparing the *trimeni* on Plate XVIII, Fig. 1, with the *hippocoön* in Fig. 2, and the *cenea* in Fig. 3,—all *polytrophus* forms from the Escarpment,—it is at once seen that the change from the apical half of the fore-wing of the ancestral form to that of *cenea* is nearly as simple as the change to *hippocoön*. For the rest of the pattern, *cenea* requires only a more widespread invasion of black than *hippocoön*. There are six examples of *polytrophus* ♀ f. *cenea* in the Hope Department, and all exhibit primitive characteristics in the pale tint of the chief patch of the hind-wing. In none is this buff like the Danaine models, but it is pale yellowish like *trimeni* in three, and pale yellowish with a faintly brownish tinge in the other three, including the specimen represented on Plate XVIII, Fig. 3. In five cases the chief spot of the fore-wing follows the tint of the hind-wing patch, in the sixth the chief spot is white. The other spots on fore- and hind-wings are generally pale yellowish, sometimes white. It is quite clear that we have in three specimens a stage in the transformation of the ancestral yellow tint into buff. It is of interest to observe that the pattern of the *cenea* form is completely attained in three specimens whose pale colour remains entirely ancestral. Not one of the six specimens exhibits rudimentary "tails," although the sub-marginal hind-wing spots are strongly developed. (Plate XVIII, Fig. 3.)

The *cenea* ♀ form is dominant in the sub-species *cenea* of the south and south-east, and common in *polytrophus* of the Kikuyu Escarpment. It occurs, but more rarely than *hippocoön*, in other parts of British East Africa, as a female form of *tibullus* and of the intermediate forms round

the Victoria Nyanza. It is unknown and probably entirely wanting from the sub-species *merope* on the west coast, but it may perhaps occur at the extreme eastern development of the sub-species in Uganda. Its distribution is thus co-extensive with that of its Danaine models the forms of *Amauris echeria* and *albimaculata*.

- (a) *Evidence of diaposematic mimicry between the cenea ♀ f. of P. dardanus and two species of the Danaine genus Amauris.*

It has been shown on p. 286 that the squarish shape of the large pale patch on the hind-wing of the female forms of *dardanus* is extremely ancestral, and the question arises as to whether *Amauris echeria* and *albimaculata* have not mimicked and indeed exaggerated this feature in the *Papilio* which in other respects has mimicked them. There are many reasons in favour of diaposematic relationship between *Danaine* and *Papilio*. The squarish patch in the two species of *Amauris*, although far more marked than in the *cenea* form, is in all probability a recent development. It shows remarkable synaposematic sensitiveness, losing much of its characteristic sharpness and angularity in the presence of other species of the same genus. This change may be seen by a glance at Mr. S. A. Neave's Plate IX in the present volume. *Amauris albimaculata* (♂ Fig. 2a, ♀ Fig. 3a) shows this change in the presence of *Amauris psyttaea*, form *damocloides*, ♂ Fig. 2, ♀ Fig. 3. Compare the shape of the patch in the two sexes of *albimaculata*, with that of the same species from Natal far beyond the influence of *damocloides*,—♂ Fig. 4, ♀ Fig. 5. *Amauris echeria* is also changed in the same direction by the presence of the same model, as may be seen by comparing ♂ Fig. 2b and ♀ Fig. 3b under the influence of *damocloides* (♂ Fig. 2, ♀ Fig. 3), with the same species from Natal—♂ Fig. 6, ♀ Fig. 7. *Amauris lobengula* (Plate XXII, Fig. 1), closely allied to *A. echeria* and probably ancestral to it, because less peculiar in the genus, possesses a larger hind-wing patch in which the square shape is not nearly so marked. It is in fact almost precisely similar in shape to that of the *trimeni* form shown on Plate XIX, Fig. 1, and the *hippocoon* on Plate XVIII, Fig. 2. The exaggeration of the feature in *Amauris albimaculata* and *echeria* is no reason against the hypothesis that it has been derived by mimicry. In the great majority of the forms of *Acræa*

johnstoni, undoubtedly mimetic in this respect, we meet with a still further exaggeration of the same character, the outer corner of the square being pulled out so as to form the most distinctive feature of the wing (see Plate XXI, Figs. 1*b*, 3*a*, and 4*a*, Plate XXII, Figs. 1*a* and 2*a*). That diaposematic resemblance is apt to arise between the *Papilionidæ* and the most distasteful groups in the same region has been shown by Dr. F. A. Dixey (Trans. Ent. Soc. Lond. 1896, p. 75; also 1894, p. 298) as regards S. America, and recently in a very striking manner by Mr. S. A. Neave (Trans. Ent. Soc. Lond. 1906, pp. 216-218) as regards certain other African species.

(4) *Planemoides*. Until Mr. C. A. Wiggins presented his splendid series of captures made in 1903 near the N.E. and N.W. shores of Lake Victoria Nyanza, there only existed in the Hope Department a single specimen labelled "Angola; Rogers, 1873." This specimen was, as far as I am aware, up to 1903, the unique representative of *planemoides* in European collections. There are at the present moment no less than ten examples of the form, or of intermediates between it and other forms, at Oxford,* so that it is now possible to compare *planemoides* with the other mimetic females of *dardannus* and to attempt to assign its place and suggest its past history.

It is convenient first to describe the intermediate specimens.

(a) ♀ form intermediate between *cenea* and *planemoides*.

The specimen here described is represented on Plate XX, Fig. 1. The discal patch of the hind-wing is not white as in *planemoides* but nearer to the buff of *cenea*, although with a faintly reddish-brown tinge which may perhaps indicate some influence of *trophonius*. The submarginal light spots are more developed than is usual in *planemoides*, although the example represented in Fig. 4 does not differ widely in this respect. While the hind-wings more nearly resemble the ♀ f. *cenea*, the fore-wings are on the whole much nearer to *planemoides*, as may be inferred by

* Some of these do not belong to the Hope Collection, but are the property of Mr. A. H. Harrison. They are however available for study and comparison, and two of them are represented on Plate XX, Figs. 1, 4. No less than five out of the ten examples are figured on the plates accompanying the present memoir, and a sixth by Mr. S. A. Neave on Plate X, Fig. 8.

comparing the intermediate form (Plate XX, Fig. 1) with *planemoides* represented below it (Fig. 2), and with the ♀ f. *cenea*, represented on Plate XVIII, Fig. 3. The colour of the markings is the deep rich tint of *planemoides*, not the far paler shade of *cenea*. The fusion of the three spots grouped round the outer end of the cell, and the shape of the marking thus produced, is almost precisely as in the specimen shown on Plate XX, Fig. 2; while the spreading outwards and downwards of the chief spot (below the cell) reproduces the inner marginal end of the band of *planemoides*. The central part of the band is wanting, but a tendency towards fusion can be detected in the figure and is far more evident on the specimen. The *planemoides* selected for comparison with this intermediate specimen, and shown in Fig. 2, is unusual owing to the overspreading of the white patch of the hind-wing by greyish scales. It is also a little abnormal and suggests transition towards the specimen above described (Fig. 1) in the separation of the spot within the fore-wing cell from the fulvous band (compare Figs. 3 and 4) and also in the comparative narrowness of the band itself, which is especially marked in the central portion where the discontinuity appears in Fig. 1. Figures 1 and 2 considered alone would suggest the origin of *planemoides* from the *cenea* form.

(β) ♀ form intermediate between *hippocoon* and *planemoides*.

The insect represented in Fig. 3 shows a tendency towards the *hippocoon* form in the extension of the fulvous band (representing of course the white of *hippocoon*) towards the base of the fore-wing, along the inner margin, as well as in the trace of an invasion of dark ground colour dividing the band at its centre. The effect is to produce a considerable approximation to the fore-wing pattern of *hippocoon* (Plate XVIII, Fig. 2) or even more of *trimeni* (Plate XVIII, Fig. 1). Fig. 3, on Plate XX, compared with the fine example of typical *planemoides* represented in Fig. 4 suggests the origin of the latter from *hippocoon* or *trimeni*.

(γ) ♀ form intermediate between *trophonius* and *planemoides*.

Only quite recently Mr. Harry Eltringham, F.E.S., has kindly shown me a beautiful coloured representation of a specimen from Entebbe which is intermediate between

planemoides and a *trophonius* of the western or *merope* type.* The latter strongly preponderates: the hind-wings are entirely those of *trophonius*. The fore-wings exhibit the fulvous area of *planemoides* spreading inwards along the inner margin and there becoming continuous with the fulvous area of *trophonius*. The pattern of the fore-wing is very like that represented on Plate XX, Fig. 3, but the fulvous area is somewhat larger and much less invaded by dark ground colour. The apical half of the fore-wing is typical *planemoides*, closely resembling that of the figure just quoted. This specimen taken alone would suggest the origin of *planemoides* from *trophonius*.

(δ) *Intermediates between planemoides and other mimetic female forms of dardanus, not ancestral but due to first crosses between female of one form and male representing another form.*

The three intermediate examples described above (α , β , and γ) suggest the origin of *planemoides* from the fully developed *cenea*, *hippocoon* and *trophonius* respectively; and yet it is unreasonable to suppose that *planemoides* arose from more than one of the other female forms. We are thus driven to believe that such intermediates are not necessarily ancestral and to inquire what other significance they may possess. Here we derive the greatest assistance from Mr. G. F. Leigh's breeding experiment in which it has been seen (see pp. 283, 313) that the *cenea* offspring of a *trophonius* parent exhibited distinct traces of the latter form. It will be remembered that this influence was evident in the deeper tint of the hind-wing patch in one specimen (Plate XVII, Fig. 8) and the inner marginal markings on the fore-wing of another (Fig. 11).† The intermediates described in this section of the paper are probably always the result of first crosses between females of one form and males bearing the tendencies of other female forms. We are compelled to believe that in later generations their female offspring

* Easily distinguished from the *trophonius* of the south and east by its greater size, by the marked invasion of the margin of the fulvous area on the hind-wing by internervular radii, and by the much paler shade of the fulvous areas.

† A faint trace of the same marking is to be seen in the *cenea* offspring of a *trophonius* bred by Mr. Leigh in 1903. It can be just detected in the reduced representation on Fig. 11, Plate XXXI, Trans. Ent. Soc. London, 1904.

would not remain intermediate, but would split up, in accordance with the Mendelian conception, into the parent forms; and we can thus understand the comparative rarity of intermediates. But while this is almost certainly true of the sub-species of *dardanus* in the W., S., and on the E. coast of Africa, where the specialization of the female forms has been carried to a high pitch, it is probably not equally true of the sub-species *polytrophus* of the Kikuyu Escarpment.

(ε) *Probable origin of planemoides from early variants of trimeni.*

The abundance of intermediates of all kinds among the females of *polytrophus* and the relative numbers of the ancestral form *trimeni* indicate a near approach to the origin of the diverse female forms. It is probable indeed that first-cross intermediates between the specialized forms themselves would split up into the parent forms on the Escarpment as in other parts of Africa; but it is by no means equally certain that the intermediates between each of them and their primitive ancestor *trimeni* would behave in this manner. Only thus does it seem possible to explain the relative abundance on the Escarpment of intermediates almost always exhibiting primitive characteristics, viz. some approach to *trimeni*.

It would be of the highest interest to breed any of the sub-species of *dardanus* through several generations: especially is this desirable in the case of *polytrophus*, which is certain to yield results of the utmost importance from many points of view.

It is probable that *planemoides* arose from *trimeni* by a combination of the varieties which were to produce *cenea*, *hippocoon*, and *trophonius*. The size and shape of the white hind-wing patch probably arose from varieties on the way to *cenea*, its whiteness from those which were forming *hippocoon*, while the fulvous tint of the fore-wing was a utilization in another direction of the characteristic colouring of *trophonius*.

The argument made use of with regard to *planemoides* applies to all the other mimetic female forms; for intermediates between them occasionally occur probably in every sub-species and in all parts of the area of distribution. But while such varieties are not to be looked upon as ancestral, the case is very different with the Escarpment

forms. Every one of the six *polytrophus cenca* which have come under my observation are primitive in the tint of the pale markings and we must assume that in this case we are in presence of a truly ancestral feature.

(♂) *An interesting gynandromorphic specimen of the ♀ f. planemoides.*

Although the male and the diverse female forms of the southern *P. dardanus*—the sub-species *cenca*—have been shown by direct evidence to be a single species by the important breeding experiments of Mr. G. F. Leigh, F.E.S.,* the same proof is unfortunately still wanting in other parts of Africa. It is therefore very satisfactory that other evidence has become available in the case of the most recently discovered form *planemoides*. This is in part supplied by the existence of intermediates between it and the other female forms of *dardanus*, two of which are shown on Figs. 1 and 3 on Plate XX. But still more striking evidence is supplied by a remarkable gynandromorphic specimen collected by Mr. T. T. Behrens, R.E., and represented on Plate XVIII, Fig. 4. The butterfly was obtained in 1902–3 on the west shore of the Victoria Nyanza between Entebbe and the mouth of the Kageru River. The admixture of male colouring, which is confined to the left wings, is very well represented in the figure, except upon the white patch of the hind-wing, where the pale yellow streaks could not be differentiated from the white background by photographic means. If the black ground colour of the left hind-wing be compared with that of the right, it is seen that three submarginal irregular areas of a deeper shade are present on the former wing but absent from the latter. These represent the submarginal band of the male while the spaces between them are the costal and inner gaps. The yellow male scales pass through the costal gap as an almost continuous streak, while they are developed in small scattered masses in the neighbourhood of the inner gap. The yellow scales reach the extreme margin of the hind-wing in the concavities of the scalloped border, as in the male, while the yellow of the two concavities nearest the anal angle

* Published in Trans. Ent. Soc. 1904, p. 677, and in the present memoir.

(omitting from consideration the one that has been accidentally injured) possesses a pale brownish edging also characteristic of the male.

In the fore-wing the yellow male streaks and patches are strongly developed on the disc below the cell. It is deeply interesting to observe how sharply cut off they are when, crossing the lower part of the fulvous band, they reach the black border. We are driven to infer that this portion of the border almost precisely corresponds in the two sexes and that the black border of this and other female forms is inherited unchanged from an ancestor like the male. In fact this character carries us further back than the ancestral *trimeni* form (Plate XVIII, Fig. 1) in which the male border has already been greatly modified. It is to be observed furthermore that the abrupt termination of the yellow streaks confers upon the black border a sharpness of outline entirely wanting in the female form, as is at once seen when the right and left sides are compared. Opposite to the middle of the hind margin the black border is invaded by an outward extension of the fulvous band—due to that part of it which represents the sub-apical bar of the *hippocoon* ♀ form (compare Figs. 2 and 4 on Plate XVIII). Here the ancestral male border has been much reduced, and in the gynandromorphic specimen the site of the invading fulvous concavity is in part covered by grey scales quite distinct from the yellow ones on those parts of the wing surface which are yellow in the male. The photographic method however only imperfectly renders the difference.

(η) *Mimetic relationships and distribution of planemoides.*

This beautiful form, only recently recognized as a mimic of *Planema poggei* by Trimén and Neave (Proc. Ent. Soc. Lond., Oct. 7, 1903,) is not known to occur as a female form of any sub-species of *dardanus* except *merope* (= *dardanus dardanus*). The occurrence at Taveta of a fine variety of *Acrava johnstoni* (Plate XXI, Fig. 2a) strongly convergent towards *planemoides* renders it probable that this latter exists in the neighbourhood, perhaps as one of the female forms of the sub-species *tibullus*. The immense increase in our knowledge of *planemoides* during the last two or three years encourages the hope that we shall at no distant date be fully acquainted with its range.

B. MIMETIC FORMS OF Aeræa johnstoni, Godman.

Introductory.—In the following section the attempt will be made to show that the whole series of diverse forms which have given to this species its long synonymic list has arisen through the development of mimetic likeness to several distinct models, both *Danaine* and *Acræine*. The form-names suggested by Oberthür* have been followed throughout, *Aeræa toruna*, Grose-Smith, being regarded as a form of *semifulvescens*, Oberth. In a later part of the section facts will be brought forward which appear to prove that this protean butterfly is not only conspecific with *fallax*, Rogenh. (= *kilimandjara*, Oberth.), as Aurivillius suggests, but also with Godart's species, *lycoa*.

I owe the opportunity of writing this part of the present memoir to my kind friend, the Rev. K. St. Aubyn Rogers, M.A., of Wadham College, Oxford, who has presented to the University Collection the deeply interesting series of models and mimics represented on Plate XX. The whole of the butterflies there represented together with other examples of the same mimetic forms were captured on the slopes of Kilimanjaro in 1905. In addition to this extensive material Mr. St. Aubyn Rogers has presented many examples of *A. johnstoni* from Taita and Taveta in British East Africa, including the fine and remarkable variety from the last-named locality, represented on Plate XXII, Fig. 2*a*. The series of models and mimics would however have lacked completeness if other kind friends had not also afforded valuable help:—Mr. Guy A. K. Marshall sending me an extreme south-eastern form (Plate XXII, Figs. 1*a*, 1*b*) with its model (Fig. 1); and Mr. C. A. Wiggins the extreme western mimetic form (Plate XXII, Fig. 3*a*) with the model (Fig. 3) from the same district.

The mimetic resemblance of the commonest forms of *A. johnstoni* (*proteina* and *flavescens*) to *Danaine* butterflies of the genus *Amauris* was suggested by the present writer in 1897.† Although greatly impressed by the likeness of *Acræine* to *Danaine*, I was then quite unaware of the existence of this wonderful range of forms and of the

* *Études d'Entomologie*: Dix-septième Livr.: Avril 1893.

† "Theories of Mimicry, as illustrated by African Butterflies," read before Section D of the British Association at Toronto, Aug. 20, 1897. Abstract in Report of the Toronto Meeting, pp. 688-691.

striking example of Müllerian mimicry which it was to supply.

I. *Mimetic forms of* *Acræa johnstoni*, *Godman*.

It is now proposed to consider the various often widely-separated forms of *johnstoni* in the probable order of their evolution in time, and to point out the models in each case.

(1) *Acræa johnstoni*, Godm., form *proteina*, Oberth. Oberthür (Etudes D'Entomologie: Dix-septième Livr.: Avril 1893: Pl. II, Fig. 14) considers the variety with white spots in the fore-wing and a squarish pale buff discal patch in the hind-wing as the typical form of the species; and it is probably more ancestral than any other. It appears to be much more abundant than the buff-spotted form *flavescens*, and also to have a wider range. The most southern examples in the Hope Collection, viz. three specimens sent to me by my kind friend Mr. Guy A. K. Marshall from Chirinda Forest, Gazaland, in S.E. Rhodesia (4000 feet), are all of this form, and it is also far more numerous than any other in the Rev. K. St. Aubyn Rogers' series from the Kilimanjaro district, as also in the series from the Tiriki Hills on the N.E. shores of the Victoria Nyanza (5100 feet) kindly given me by Mr. C. A. Wiggins.

The *proteina* form is an obvious and beautiful mimic of *Amauris albimaculata* and the white-spotted forms of *Amauris echeria*. Its synaposematic sensitiveness is well seen in Mr. Marshall's specimens from Chirinda in which the squarish discal patch of the hind-wing is unusually large, clearly as an approach to *Amauris lobengula* (Plate XXII, Fig. 1), one of the dominant Danaines of this locality. The discal expansion is more pronounced in the female *Acræa* (Fig. 1*b*) than in the two males, one of which is represented in Fig. 1*a*. The more perfect mimetic likeness of the female is an example of the well-known and widely applicable principle explained by A. R. Wallace.*

The resemblance of *proteina* to the Danaine model is far less perfect on the under-side, although the spots of the fore-wing and the patch of the hind-wing are still the prominent features. The ground colour in the marginal

* Trans. Linn. Soc., vol. xxv, 1866, Pt. I, 1865, p. 22. See also Poulton in Linn. Soc. Journ. Zool., vol. xxvi, pp. 580-582.

part of the hind-wing and the apical part of the fore-wing is marked by alternating dark and light stripes,—dark veins, paler ground colour and again darker internervular radii. This is certainly the conspicuous feature of the insect during prolonged rest with closed wings hanging downwards, and it is an appearance characteristic of many *Acræinæ*.* Hence in complete rest the prominent characters are synaposematic with other *Acræinæ*; during flight and in brief rests with wings open the characters are synaposematic with the genus *Amauris*.

Oberthür's form *semialbescens* (l. c., Plate III, Fig. 29) with white spots on the fore-wings and reddish-brown hind-wings bearing a paler discal patch of the same colour, may be looked upon as an exceptional variety of *proteina*. It is of much interest as an example of the variational material out of which natural selection has probably produced such mimetic forms as *fulvescens* (Plate XXI Fig. 4a), and *toruna* (Plate XXII, Fig. 3a.)

(2) *Acræa johnstoni*, form *flavescens*, Oberthür (l. c., Pl. I, f. 4). This form differs in the spots of the fore-wing being buff instead of white. It is an obvious mimic of the buff-spotted forms of *Amauris ccheria*. Every gradational shade between pronounced buff and the pure white of *proteina* is to be found. A good intermediate example is figured on Plate XXI, Fig. 1b, but the methods of photography do not at present enable us to distinguish between these pale tints. The remarks upon the under-side colouring of *proteina* apply equally to *flavescens*.

(3) *Acræa johnstoni*, form *semifulvescens*, Oberthür (l. c., Pl. II, f. 19). This is the form of the species described by Godman from Kilimanjaro, and therefore from the systematist's point of view the type of the species. From every other point of view it is evidently highly specialized—a comparatively modern offshoot from the ancestral *Amauris*-mimicking forms *proteina* or *flavescens*. The change has been brought about by selection in the direction of other models, Acraeine in place of Danaïne. There are at least three different sub-forms included under *semi-*

* It is also reproduced in the mimicry of *Acræinæ*, e. g. in the males of certain species of *Pseudacræa*. In the magnificent W. African Lycaenid, *Epitola honorius*, F., the portions of the under-side exposed in prolonged rest are beautifully mimetic of this Acraeine appearance, not only as regards the radiate markings but also in the characteristic group of black spots at the base of the hind-wing.

fulvescens, each of the three mimicking a different Acraeine species or form.

(a) The most primitive sub-form is typical *semifulvescens* as it occurs on Kilimanjaro,—represented in Plate XXI, Fig. 3a. The whole of the fore-wings, within the zigzag line of the four spots, is bright fulvous, while the discal patch of the hind-wings is pale yellowish. Thus is produced a considerable superficial resemblance to *Planema quadricolor*,* Rogenh., from the same mountain (Fig. 3). The zigzag line of pale spots bordering the fulvous area of the fore-wings represents the black margined fulvous band which borders the deep rich brown of the *Planema*. The relative position of darker and lighter shades is the same, although the inner half of the surface is much brighter in the mimic than in the model. In the hind-wing the *semifulvescens* form has a far larger pale area than the *Planema*, in which the rich brown black-spotted triangular basal patch of the under-side is reproduced upon the upper. The discal band of the *Planema*, if smaller than the squarish patch of the mimic, is brighter in tint, being white instead of pale yellow. In one specimen of *semifulvescens* from Kilimanjaro the black ground colour has greatly encroached upon the basal margin of the discal patch, leaving a pale band which closely approximates to the form of the marking in the *Planema*.

(β) The second sub-form of *semifulvescens* (Plate XXII, Fig. 2a) is a splendid member of the group of mimics clustered round *Planema poggei* (Fig. 2) as the central model,—the combination of which so many members have been described and figured by Mr. S. A. Neave (Trans. Ent. Soc. 1906, p. 218: Plate X). It differs from Oberthür's form (a) in the restriction of the fulvous area of the fore-wing to the neighbourhood of the zigzag line of pale spots (compare Plate XXII, Fig. 2a, with XXI, Fig. 3a). On the distal side of each spot as in *semifulvescens* the ground colour of the wing is black; but it is also very dark brown, almost black, on the proximal side of the innermost spot, except along the costa, where the fulvous tint extends nearly to the base of the wing. The discal patch of the hind-wing is moreover white instead of

* This *Planema*, of which a male and a female were presented by Rev. K. St. Aubyn Rogers, was new to the Hope Collection, and is unrepresented in the National Collection. It was kindly named for me from a photograph by Prof. Chr. Aurivillius.

pale buff. The resemblance of this striking and beautiful form is also promoted by its size; for it is one of the largest specimens of *johnstoni* which I have ever seen. As in so many other cases this mimic is an even closer approach to a co-mimic than it is to the primary model. And of all the species which are grouped round *Planema poggei* there can be no doubt that its resemblance is strongest to the *planemoides* female of *Papilio dardanus* (Plate XX, Figs. 2, 4). I do not know of this latter from Taveta where the (β) form of *semifulvescens* was collected by Mr. St. Aubyn Rogers; but *planemoides* exists in the A. H. Harrison collection from Nairobi, so that its existence in the neighbourhood of Kilimanjaro and Taveta is at any rate probable; and the same may be said of *Planema poggei*, the primary model, also labelled Nairobi in the same collection.

In both (α) and (β) sub-forms of *semifulvescens* the fulvous part of the fore-wing under-side would be hidden by the hind in the attitude of prolonged rest, so that the appearance becomes synaposematic with many of the smaller *Acræinæ* rather than with the particular *Planema* models. On the other hand, in flight and probably during brief rest between successive flights the basal part of the fore-wing under-side would contribute to the visible appearance and serve to reinforce the resemblance to the *Planemas*.

(γ) The third sub-form of *semifulvescens* is the *toruna* form (Plate XXII, Fig. 3a), described under that name from Toro, W. Uganda, by Mr. H. Grose-Smith. There can be no doubt I think that this is a further development of the form described by Oberthür from Kilimanjaro—a modification brought about by mimetic resemblance to another *Planema* model,—*P. latifasciata*, E. M. Sharpe (Plate XXII, Fig. 3). It is altogether a much more perfect mimic of this *Planema* than *semifulvescens* (α) is of the allied *P. quadricolor*. The rich brown colour of the basal half of the fore-wing is here alike in model and mimic, while the zigzag row of four spots tend in *toruna* to fuse and generally completely fuse into a zigzag fulvous band somewhat resembling but more irregular than that of the *Planema* model. In *P. latifasciata* the black inner border of the fulvous band is far more feebly developed than in *P. quadricolor*, so that the absence of this border in *toruna* does not greatly detract from the likeness. On the other hand, the fulvous band itself is far wider and more con-

spicuous in *latifasciata*, and this is well matched except in form by the mimic. In fresh specimens moreover the ground colour of both wings in the Toro model and mimic is of a distinctly brownish shade of black, wanting in the dark ground of the more eastern pair. The discal band of the hind-wing in *P. latifasciata* (Plate XXII, Fig. 3) is fulvous and broader than the white band of *quadricolor* (Plate XXI, Fig. 3): the triangular basal brown patch of the hind-wing under-side is reproduced above in both species of *Planema*, but the black spots are indistinctly seen on the upper-side of *latifasciata*, while the chief members of the group are conspicuous, being in fact reproduced on the upper-side of *quadricolor*. In *toruna* the discal patch on the hind-wing is fulvous, and the effect at a little distance is singularly like that of the model. It is however produced in a different way; for the uniform bright fulvous tint of *latifasciata* is imitated by a fusion of two distinct colour elements in *toruna*,—viz. the paler fulvous ground colour of the patch and the deep fulvous internervular and intracellular rays which traverse it. The shape of the discal patch has also been modified into close resemblance to the band of *latifasciata*, although a trace of the angle, so well known and conspicuous in the forms of *johnstoni*, remains as a guide, indicating the path of evolution. The basal invasion by deep rich brown of the pale patch on the hind-wing suggests the basal triangular area of the *Planema* model. On the under-side the patterns of both model and mimic are reproduced in paler shades, still maintaining their close resemblance. The discal band of the hind-wing of *Planema* and the corresponding patch of the *Acræa* are white, and in the latter the characteristic squarish shape is far more prominent than on the upper-side. The basal spots of the hind-wing under-side which are so concentrated towards the base in other forms of *johnstoni* are here moved outwards and are placed upon and along the borders of a rich brown triangular area resembling but much smaller than that of the model. The *toruna* form of *johnstoni* is one of the most interesting of the mimetic appearances developed by this remarkable and protean species.

(4) *Acræa johnstoni*, form *fulvescens*, Oberthür (l. c., Pl. II, f. 21). This, the last of a wonderful series, is one of the most remarkable, the black ground colour persisting only as

a narrow margin widened at the apex of the fore-wing (Plate XXI, Fig. 4a). The whole of the rest of the surface of both wings is bright fulvous, with the four spots of the fore-wing and the squarish patch of the hind-wing visible (especially the former) as a paler shade of the same colour. At a little distance and during flight these markings would become inconspicuous, and the butterfly would closely resemble a small specimen of the form of *Limnas chrysippus* dominant in British East Africa, viz. the *dorippus* form (= *klugii*), without the black and white apex to the fore-wing (Plate XXI, Fig. 4). On the under-side the resemblance of *fulvescens* to the primary model is less close because of the absence of the distinct black margin so conspicuous on the upper-side. But this very appearance, together with a radially striped pattern caused by the alternation of dark veins and brighter ground colour, and the increased paleness of the marginal part of the hind-wing and the apical area of the fore-wing, promote a deuterostynposematic resemblance to another Acraeine mimetic of *dorippus*,—the *daira* form of *Acræa encedon*. These two Acraeas are moreover of nearly the same size, while the Danaeine primary model is of course a far larger butterfly. The chief basal spots of the hind-wing under-side are not black and prominent but dark fulvous and therefore inconspicuous, in this case producing an appearance suggestive of *dorippus*, and unlike any of the forms of *encedon* in which the black spots are so conspicuous a feature.

II. *Acræa johnstoni*, Godm., and *A. fallax*, Rogenh., the eastern forms of *A. lycoa*, Godt.

The three forms which it is here proposed to unite under a single species are thus grouped by Aurivillius: *—

"109. *Acræa johnstoni*, Godm.; *telekiana*, Rogenh.; *fulvescens*, Oberth.; *semifulvescens*, Oberth.; ab. Octobalia, Karsch.; ab. (et var.) *confusa*, Rogenh.; *johnstoni*, Butl.; *protina*, Oberth.; *flavescens*, Oberth.; *semialbescentis*, Oberth.

"110. *A. fallax*, Rogenh., forma præcedentis?; *Kili-mandjara*, Oberth.

"111. *A. lycoa*, God.; ab. ♀ *Butleri*, n. ab. *lycoa*, var. ♀ *Butl.*"

* Rhop. Æthiop. 1898, pp. 114, 115. References are omitted from the quotation. The italics indicate synonyms.

We see therefore that Aurivillius keeps *A. lycoa* distinct, while he suggests that *A. fallax* (*kilimandjara*) may be a form of *johnstoni*. I believe that he is right in this last opinion, although positive proof can only be gained by breeding; but the facts set forth below render it certain that *fallax* is the eastern form of *lycoa*. If Aurivillius is right in his association of *fallax* it will inevitably follow that the whole series of varied forms must fall under Godart's species,—*lycoa*.

Acraea lycoa of the tropical west coast is distinguished from *A. johnstoni* by the following characteristics:—

(1) The large size of the four spots on the fore-wing and the tendency of the subapical pair to fuse and form a subapical bar: the tendency of the more interior pair similarly to form a patch extending from below the end of the cell towards but not quite reaching the posterior angle of the wing. The spots are, however, sometimes separate, although much larger and more nearly approximated than in *johnstoni*.

(2) The pronounced sexual dimorphism of which no trace can be found in *johnstoni*. The males of *lycoa* have a much browner ground colour than the females, especially in the hind-wing, while the spots of the fore-wing are pale buff instead of white and are sometimes evanescent. Furthermore the white discal patch of the hind-wing is unrepresented in those males I have had the opportunity of examining, while the development of the internervular radii is correspondingly increased.

(3) The apex of the fore-wing of *lycoa* is more broadly rounded and the costal margin more curved than in *johnstoni*. The outline of the wing between the apex and the posterior angle is straight or even convex in the females, straight or very slightly concave in the males. In *A. johnstoni* it is probably always concave, although sometimes very slightly so.

(4) The basal black spots on hind-wing under-side are smaller in *lycoa* and less concentrated towards the extreme base of the wing. The spot in the base of the cell with the two spots on the costal side of it forms in *lycoa* a characteristic approximately equilateral triangle. Owing to the greater concentration of spots the corresponding triangle in *johnstoni* is nearly always isosceles with its base towards the root of the wing. It is moreover less conspicuous as a feature in the wing of this latter form.

(5) The discal *white* patch on the hind-wing of the female *lycoa* is somewhat larger than in *johnstoni*: moreover it is rounded and not subquadrangular as is the *buff* patch of the eastern form, although rare exceptions both as regards contour and tint are not wanting in the latter. The rounded margin of this patch in the female *lycoa* is more invaded by internervular radii than in *johnstoni*, and consequently less sharply defined. Outside the discal patch the strong development of these dark radii contrasted with the paler (greyish or rarely brown) ground colour produces a very different effect from the almost uniformly dark appearance of the corresponding area in *johnstoni*.

When we reach the western part of Uganda, in the uplands of Toro, at a height of 7-9000 feet, *lycoa* is still a dominant *Acræa*. The only male I have seen resembles the western form except that there is a slight tendency towards the development of a buff discal patch in the hind-wing. Some of the females resemble those of the west coast except that the white discal patch is very slightly smaller: in others the four white spots of the fore-wing are widely separated and smaller, approaching the condition of *johnstoni*, while in these very individuals the discal patch of the hind-wing is smaller and more sharply defined. In all other respects the western characters described above are still maintained.

Passing still further east to the N.W. shore of the Victoria Nyanza at Entebbe, we find that the males have now gained the four widely separated buff spots in the fore-wing, not nearly so distinct and sharply defined as those of *johnstoni*, but otherwise very similar. Many individuals have a small trace of the buff discal patch. All the females I have seen resemble the most *johnstoni*-like of those from Toro, except for the tint of the discal patch of the hind-wing, which has become a very pale buff. These females are nearly indistinguishable from the *kilimandjara* figured by Oberthür * (= *fallax*, Rogenh.). Owing to the kindness of my friend, Mr. T. T. Behrens, R.E., I have had the opportunity of examining a pair of this form from the Anglo-German boundary west of the Lake, but not more than sixty miles from it. While the female resembles those from Entebbe, the male has a far

* Etudes D'Entomologie: Dix-septième Livr.: Avr. 1893, Pl. II, f. 17.

more marked but very imperfectly defined buff discal patch.

We now pass to the N.E. shore of the lake. The Hope Department possesses an interesting series of specimens kindly presented by Mr. C. A. Wiggins. They come from the Tiriki Hills, 5100 feet, twenty miles N. of Kisumu. In the more defined buff discal patch of the hind-wing the three males are a further advance in the direction of the *fallax* form than that reached by any male I have seen from further west. In the four females the discal patch is slightly less pale than that of any as yet mentioned, while the rest of the hind-wing is more uniformly dark. They are in fact almost precisely similar to females of the *kilimanjara* form (see Plate XXI, Fig. 2a) from the mountain after which it was named by Oberthür; only differing in the *smaller* size of the discal patch and its slightly paler tint. A single female obtained by Mr. Wiggins at Kakamega's (5500 ft.) near Mumias on the Uganda Railway, about fifteen miles N.E. of Kisumu, is of the same type, but the patch is even smaller and very slightly deeper in tint. Mr. C. A. Wiggins' Nyanza and Toro specimens were identified as forms of *A. lycoa* by Mr. S. A. Neave (Nov. Zool., vol. xi, March 1904, pp. 348, 349), and I find that the same forms from Toro and Nyangori are labelled "*lycoa*?" by Miss E. M. Sharpe in the A. H. Harrison Collection.

We now pass to the most eastern specimens I have examined, viz. those kindly sent me by Rev. K. St. Aubyn Rogers from Taita, Taveta, and Kilimanjaro. In these forms the buff-spotted males with an enlarged discal patch of pronounced buff (Plate XXI, Fig. 1a) mimic the buff-spotted and buff-patched *Amauris echeria*, while the white-spotted females (Plate XXI, Fig. 2a) with slightly paler buff patches, also enlarged as compared with the Nyanza forms, mimic *Amauris albimaculata* and the white-spotted forms of *A. echeria*. They are certainly Rogenhofer's *fallax* and Oberthür's *kilimanjara*. They are equally undoubtedly the eastern forms of *Aerava lycoa*, modified by the mimicry of Danaines not known on the west coast. The sexual dimorphism of *lycoa* persists in *fallax*, and remains of the same kind though very different in degree; for, as pointed out above, the males bear buff spots on the fore-wing and the females white, while the discal patch is paler in the latter sex. The *johnstoni* of

Godman (*protæna* of Oberthür) differs from *fallax* and *lycoa* in that it is not sexually dimorphic. I have found males and females both present in the *semifulvescens* form and the white-spotted *Amauris*-like forms. Both sexes would probably be found in a sufficient series of any variety. It also differs in possessing squarish as compared with a rounded discal hind-wing patch, which is also more sharply defined because less invaded by internervular radii. In *fallax* the contour of the fore-wing has greatly approximated from *lycoa* towards *johnstoni*, but the apex is still slightly more broadly rounded, and the costa of the fore-wing rather more bent. On the other hand, a concavity between the apex and the posterior angle, although faint or absent in the females, has now become distinct in the males of *fallax*,—as distinct as in *johnstoni*. In this respect and the more uniformly dark ground colour of the hind-wing outside the discal patch these extreme eastern forms of *lycoa* show an approach to *johnstoni*. The basal spots of the hind-wing under-side remain however precisely those of the western *lycoa*.

A most curious change in *lycoa* as we advance from west to east is the shrinkage of the discal patch to a minimum at the N.E. of the Victoria Nyanza and its subsequent slight expansion further east.

In the collections I have already mentioned supplied by the generosity of many friends *Acræa johnstoni* was first found (in about equal numbers) accompanying the forms of *lycoa* (*fallax*) in the Tiriki Hills; and in far greater numbers at Kilimanjaro, Taveta, and Taita. The great majority are easily separated from the *lycoa* (*fallax*) forms by the characters already mentioned but intermediate individuals certainly occur. The most striking of these appeared among four males sent to me from the Kenya District by my friends Mr. and Mrs. S. L. Hinde. Of three specimens captured on February 8, 1903, at Fort Hall (about 4000 feet) two are obvious *johnstoni* while the third possesses a well-defined buff patch intermediate in outline between *fallax* and *johnstoni*. The basal spots of the hind-wing under-side resemble those of *fallax*. On the other hand, the spots of the fore-wing are white and not buff as in the males of *fallax*. The fourth specimen, captured above the Goura River (5–7000 feet) February 21, 1903, is somewhat nearer to *fallax* and the fore-wing spots are buff. A very fine intermediate example also exists in

the National Collection. In view of these intermediate specimens, and the variation in all the distinguishing characters observed when a sufficiently long series of *johnstoni* are examined I do not doubt that Aurivillius is correct in suggesting that *fallax* is conspecific with *johnstoni*. Strong support is also afforded to Aurivillius' suggestion by the observations of Rev. K. St. Aubyn Rogers, who knows both *johnstoni* and *fallax* in life in their natural habitat and looks upon them as a single species. It has been shown here that *fallax* is undoubtedly the eastern form of *lycoa*. It therefore becomes extremely probable that the whole wonderful series of forms—many of them totally unlike—associated under the name *johnstoni*, or as it was still more appropriately named by Oberthür, *proteina*, are all of them specifically identical with Godart's species *lycoa*. Furthermore, this remarkable series must be still further extended to include the *toruna* of Grose-Smith.

In conclusion, it is possible to attempt to reconstruct the history of the changes through which *lycoa* and its descendants have passed. It is probable that the male of the western *lycoa* represents the ancestral form of the whole group,—a semi-transparent fuscous and brownish *Acræa* with ill-defined markings. As regards the semi-transparency it is noteworthy that the character tends to crop up not uncommonly in the most modified form *johnstoni*, where it is often seen in the discal patch of the hind-wing. The female of the western *lycoa* became modified by synaposematic approach to the black and white species of the Danaine genus *Amauris* on the west coast. The same is substantially true of the species in Western Uganda where the black and white *Amauris* are still predominant and have even drawn the *echeria* and *albimaculata* types of their own genus after them. (See S. A. Neave in Trans. Ent. Soc. 1906, pp. 208–210.) As we go further east however these latter types become themselves predominant, and the *fallax* forms of *lycoa* follow them, the males becoming strongly mimetic and approaching the buff-spotted Danaine models, while the females still retain the ancestral colour and resemble those that are white-spotted. As regards the hind-wing both sexes gain a buff discal patch similar in colour but not in shape to the models. Finally, from the most strongly-marked of these eastern forms with the deepest shade of ground

colour there probably arose still more perfect mimics of the same models in *proteina* and *flavescens*, the two forms of *johnstoni* which are nearest to *fallax*. It is to be observed that the change in the shape of the fore-wing which occurred as *fallax* gave rise to *johnstoni* is in the direction of the form of the Danaïne and *Planema* models. *Johnstoni* once formed, variation in other directions, guided by natural selection, led to the mimicry of various additional Danaïne and Acræine models:— of *Limnas chrysippus*, var. *dorippus*, of *Planema quadricolor*, *Planema latifasciata*, and *Planema poggei*.

[My friend Mr. Guy A. K. Marshall has kindly read through the proof-sheets of this paper, and has made many valuable suggestions.]

EXPLANATION OF PLATE XVII.

The offspring of a *trophonius* form of *Papilio dardanus*, sub-sp. *cenea*, observed laying eggs on May 4, 1904, at Bellair, five miles from Durban, Natal. The observation was made and the eggs collected by Mr. G. F. Leigh, but the female parent escaped. The figures represent eleven out of the thirteen offspring bred by Mr. Leigh from these eggs at Durban. The specimens are in the Hope Department, Oxford University Museum.

All the figures are about $\frac{2}{3}$ of the natural size.

FIG. 1. Male offspring: pupated July 4, 1904; emerged August 5. The 10th to emerge. In this specimen the submarginal black band of the hind-wing is the least developed. There is however a slight trace of a narrow "sickle" partially closing the costal gap.

2. Male offspring: pupated June 26, 1904; emerged July 31. The 8th to emerge. The costal gap closed by a narrow "sickle."

3. Male offspring: pupated June 14, 1904; emerged July 25. The 5th to emerge. Although the costal gap is open there are traces of a black mark partially closing the inner gap.

4. Male offspring: pupated June 12, 1904; emerged July 18. The 4th to emerge. Very similar to Fig. 3, but the costal gap is here completely closed.

In this figure and the two succeeding it is seen that the inner border of the black margin of the fore-wing is distinctly serrated, recalling the appearance of *meriones*.

5. Male offspring: pupated June 10, 1904; emerged July 5. The 2nd to emerge. Submarginal band of hind-wing slightly more developed, and the gaps slightly less than in Fig. 4.

The *meriones*-like serration described under Fig. 4 here reaches its maximum development.

6. Male offspring: pupated June 16, 1904; emerged July 27. The 6th to emerge. Hind-wing far more heavily marked than in any other of the male offspring, both gaps being completely closed. These males, emerging in July and August 1904, are as a whole far less heavily marked than those bred in November 1902 and November 1903, by Mr. G. F. Leigh.

- FIG. 7. Female offspring, *trophonius* form : pupated July 6, 1904 ; emerged August 26. The 13th to emerge. A typical example of the southern form of *trophonius*, here for the first time bred from a *trophonius* female parent.
8. Female offspring, *cenea* form : pupated June 12, 1904 ; emerged July 17. The 3rd to emerge. The discal patch on the hind-wing is distinctly browner than usual,—a result of *trophonius* parentage appearing in an otherwise typical *cenea* ♀ form.
9. Female offspring, *cenea* form : pupated June 22, 1904 ; emerged July 29. The 7th to emerge.
10. Female offspring, *cenea* form : pupated July 8, 1904 ; emerged August 24. The 11th to emerge. The right-hand wings, being somewhat crippled, are only partially shown in the figure.
11. Female offspring, *cenea* form : pupated June 11, 1904 ; emerged July 4. The 1st to emerge. The shape of the principal spot of the fore-wing, and the development of a light patch on its inner margin, as well as the evident tendency of the two markings to fuse, show a distinct influence of the *trophonius* parentage.

EXPLANATION OF PLATE XVIII.

Female forms of *Papilio dardannus*.

All the figures are about the natural size. The butterflies were intended to be precisely of the natural size, but as a matter of fact they are all slightly enlarged. Furthermore, probably in consequence of the concurrence of minute errors, the figures on the right side, 3 and 4, are rather more magnified than those on the left, 1 and 2. The error is well within the limits of individual variation.

- FIG. 1. *Papilio dardannus*, sub-sp. *polytrophus*, ♀ f. *trimeni*, n. f. Kikuyu Escarpment, British East Africa, 6500–9000 feet. W. Doherty, October–November 1900 : in the Hope Department, Oxford University Museum. The specimen shows distinct rudimentary “tails” to the hind-wing. The pale tints are yellow and not white, while the pattern is also very ancestral as compared with the *hippocoon* form from the same locality (Fig. 2).

- FIG. 2. *Papilio dardanus*, sub-sp. *polytrophus*, ♀ f. *hippocoon*: data as in Fig. 1, except that the specimen was captured September—October 1900. Although far more specialized by mimicry of the black and white *Amauris niavius* form *dominicanus*, the origin of the pattern from that of the *trimeni* form (Fig. 1) is clear and simple. It is accompanied by a change of the pale markings from yellow to white.
3. *Papilio dardanus*, sub-sp. *polytrophus*, ♀ f. *cenea*: data as in Fig. 2. This form is far more specialized, viz. further from the ancestral pattern still borne by the male insect (Plate XVII, Figs. 1–6), than the *hippocoon* (Fig. 2). At the same time it is by no means difficult to trace the independent origin of the *cenea* from the *trimeni* form by the spreading of the black ground colour.
4. *Papilio dardanus*, sub-sp. *merope*, ♀ f. *placmoides*, partially gynandromorphic on the left side. The male influence is not only seen in the conspicuous patches and streaks of pale yellow scales on both fore- and hind-wing, but also in the traces of the three submarginal black patches on the hind-wing (compare Plate XVII, Fig. 1). These are inconspicuous because placed on a dark ground; but they can be at once recognized by comparing the left with the right hind-wing which exhibits no trace of gynandromorphism. The pale markings on the right fore-wing were caused by accidental injury and are in no way comparable with the appearance on the left side due to the existence of yellow scales like those of the male. This interesting specimen was collected by Mr. T. T. Behrens, R.E., in Buddu, on the west shore of Lake Victoria, Nyanza, between Entebbe and the mouth of the Kageru River: December 3, 1902—March 1, 1903.
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EXPLANATION OF PLATE XIX.

Ancestral females of *Papilio dardanus*.

All the figures are about $\frac{9}{16}$ of the natural size.

FIG. 1. *Papilio dardanus*, sub-sp. *tibullus*, ♀ f. *trimeni*, n. f.

Zanzibar, Lient. Turner, 1884: in the Hope Department, Oxford University Museum.

In this highly ancestral form of female the colour of the central part of the wings is not so white as in the *hippocoön* form, but very pale buff and thus far nearer to the colour of the male. The subapical patch is also imperfectly divided from the main pale patch of the fore-wing.

2. *Papilio dardanus*, sub-sp. *merope*, ♀ f. *hippocoön*.

Gaboon, Hewitson Coll., in Brit. Mus.

The exceptional variety of the *hippocoön* form here figured exhibits distinct rudiments of "tails" to the hind-wings. It is of much interest that this ancestral character should be associated with the ancestral pattern of the *hippocoön* form.

3. *Papilio dardanus*, sub-sp. *merope*, ♀ f. *hippocoön*.

W. Africa, Crowley Coll., in Brit. Mus.

This specimen of *hippocoön* also exhibits traces of the lost 'tails,' although to a much less extent than in the last figured specimen.

EXPLANATION OF PLATE XX.

Planemoides females of *Papilio dardanus* together with intermediates between this and the other female forms.

All figures are about $\frac{2}{3}$ of the natural size.

- FIG. 1. *Papilio dardanus*, sub-sp. *merope*, ♀ form intermediate between *cenea* and *planemoides*. In coll. A. H. Harrison, from Unyori, N.E. of Kisumu, about 1903. The specimen figured is beautifully intermediate between these two ♀ forms, of which the *planemoides* is seen in Figs. 2 and 4 and the *cenea* in Plate XVIII, Fig. 3. The discal patch of the hind-wing of this intermediate variety is not white as in *planemoides*. It is much nearer to the buff of *cenea*, but exhibits a faint reddish tinge which may indicate some influence of *trophonius*. Taken alone the specimen here represented would strongly suggest the origin of *planemoides* from *cenea*.
2. *Papilio dardanus*, sub-sp. *merope*, ♀ f. *planemoides*. Nyangori (Forest land), N.E. of Lake Victoria Nyanza, near Kisumu, 5000 feet. Captured November 1-8, 1902, by C. A. Wiggins. In Hope Department, Oxford University Museum. In everything except a curious overspreading of the discal patch of the hind-wings by dark scales this is a typical *planemoides* form.
3. *Papilio dardanus*, sub-sp. *merope*, ♀ f. *planemoides*, tending somewhat in the direction of *hippocoön*. From the same locality as Fig. 2. Collected about 1903 by A. H. Harrison. In Hope Department, Oxford University Museum. The *hippocoön* influence is seen in the great extension of the fulvous area along the inner margin of the fore-wing. This specimen taken alone suggests the origin of *planemoides* from *hippocoön* or *trimeni*. Compare Figs. 2 and 4 with 3.
4. *Papilio dardanus*, sub-sp. *merope*, ♀ f. *planemoides*. Nairobi, British East Africa, May 17, 1903. In coll. A. H. Harrison. The specimen figured is a fine typical example of this beautiful form. The extended basal black area of the hind-wing is an approach towards the much greater development of this marking in the model, *Planema poggei*.

EXPLANATION OF PLATE XXI.

Forms of *Acræa johnstoni*, together with their *Danaine* and *Acræine* models, from the slopes of Kilimanjaro, 1905.

The whole of the specimens figured, models as well as mimics, were presented to the Hope Department by Rev. K. St. Aubyn Rogers.

All the figures are about $\frac{2}{15}$ of the natural size.

FIG. 1. *Amauris echeria*, Boisd., ♂. The three largest spots of fore-wing and submarginal spots of hind-wing are buff-coloured: the submarginal and costal spots of fore-wing much paler buff, almost white. December 15-31, 1905: native collector.

- 1a. *Acræa johnstoni*, form *fallax*, Rogenh. (= *kilimandjara* Oberth.), ♂. *Fallax* differs from the *flavescens* (Fig. 1b) and *proteina* (Plate XXII, 1a, 1b) forms mainly in the broader, rounder apex of the fore-wing, the rounded instead of the squarish discal patch of hind-wing, and in the sexual dimorphism,—the males of *fallax* (Plate XXI, 1a) having buff spots in the fore-wing, the females (Fig. 2a) white. Furthermore the rounded discal patch of the hind-wing is here well seen to be indistinctly defined owing to the invasion of dark internervular rays, while the squarish patch of *flavescens* and *proteina* is sharply outlined. Intermediate forms occur, and there can be little doubt that Aurivillius is right in suggesting that *fallax* is a form of *johnstoni*.

The male of *fallax* with buff-spots in the fore-wing is seen to be an excellent mimic of the buff-spotted forms of *Amauris* such as that represented in Fig. 1.

The specimen shown in Fig. 1a was captured December 15-31, 1905, by a native collector.

- 1b. *Acræa johnstoni*, form *flavescens*, Oberth. The individual represented possesses very pale buff spots in the fore-wing, much paler than those of the male *fallax* (Fig. 1a). Specimens of *flavescens* however often possess spots of a pronounced shade. The individual shown in Fig. 1b is a mimic of *Amauris echeria* (Fig. 1), but as regards the pale spots is transitional towards the mimics of

Amauris albimaculata (Fig. 2), viz. the white-spotted *proteina* forms (Plate XXII, Figs. 1a, 1b), and towards the female of *fallax* represented in the next figure.

The hind-wing of *flavescens* (Fig. 1b) is seen to present a far more perfect resemblance to the Danaine models (Fig. 1, 2) than that of *fallax* (Figs. 1a, 2a). The superiority is brought about by a characteristically squarish buff discal patch which is sharply outlined and exhibits hardly any invasion of marginal rays. December 15-31, 1905 : native collector.

FIG. 2. *Amauris albimaculata*, Butl., ♀. In this specimen all the spots of both wings are pure white, the only buff marking being the discal patch of the hind-wing. December 15-31, 1905 : native collector.

2a. *Acræa johnstoni*, form *fallax*, Rogenh., ♀. The white-spotted female of this form is beautifully mimetic of the Danaine shown in Fig. 2. The discal patch of the hind-wing is however very similar to that of the buff-spotted male represented in Fig. 1a and like it less markedly mimetic than either the *flavescens* (Fig. 1b) or *proteina* (Plate XXII, Figs. 1a, 1b) forms. December 15-31, 1905 : native collector.

3. *Planema quadricolor*, Rogenh., ♂, the model of the *semifulvescens*, Oberth., form of *Acræa johnstoni* shown in Fig. 3a. The basal area of the hind-wing and the inner half of the fore-wing,—viz., the whole of its area on the basal side of the black-margined curved fulvous subapical band,—are of a deep rich brown hardly to be distinguished from black by photographic methods and therefore barely recognizable in the figure. N.E. slopes of Kilimanjaro, about 5000 feet ; State of Mamba : September 25, 1905 : Rev. K. St. Aubyn Rogers.

3a. *Acræa johnstoni*, form *semifulvescens*, Oberth., ♂. The four characteristic spots, pale yellow in tint, lie on the borders of the fulvous inner area of the fore-wing ; thus suggesting a likeness to the model (Fig. 3), where the inner area is also separated by a subapical bar of lighter tint from the black apical region. The pale yellowish discal patch of the hind-wing of course forms an area much broader than that of the model. In another specimen of this form however (Kilimanjaro, December 15-31, 1905, native collector) the basal half of this patch is almost obliterated by suffusion with ground colour, producing a much closer approximation to the hind-wing pattern of

the model. The specimen is unfortunately in too poor a condition for figuring.

Locality of specimen represented in Fig. 3a., N.E. slopes, Mamba State, about 5000 feet, September 26, 1905: Rev. K. St. Aubyn Rogers. It will be observed that the mimic was captured the day after that on which its model was taken.

FIG. 4. *Limnas chrysippus*, L., form *dorippus*, Klug. (= *klugii*, Butl.), ♀. This is the dominant form of *chrysippus* in British East Africa. Kilimanjaro, May 1905.

4a. *Acraea johnstoni*, form *fulvescens*, Oberth., ♂. An obvious and beautiful mimic of *dorippus* (Fig. 4). The ancestral markings persist, faint but distinct; and characteristic in shape and position on both wings. On the under-side they are more conspicuous. The basal spots on the hind-wing under-side are distinct, but the most prominent are in this form brown instead of black, and therefore comparatively inconspicuous. December 15-31, 1905: native collector.

EXPLANATION OF PLATE XXII.

Forms of *Acraea johnstoni* together with their Danaine and Acraëine models.

All the figures are of the natural size.

FIG. 1. *Amauris lobengula*, E. M. Sharpe, ♂, from the forest, Mt. Chirinda (about 3600 feet). Melseetter, Gazaland, S.E. Rhodesia. Captured October 7, 1905, by Guy A. K. Marshall. The model of Figs. 1a and 1b.

1a. *Acraea johnstoni*, Godm., form *proteina*, Oberth., ♂. From the same locality as the last, and captured by Mr. Marshall on the same day. The relatively large size of the squarish discal patch of the hind-wing (compare Fig. 1b on Plate XXI) is an evident synaposematic approach towards the *Amauris* represented in Fig. 1, also characterized by an especially large discal patch.

FIG. 1b. *Acræa johnstoni*, form *proteina*, ♀, from the same locality as 1 and 1a. Captured by Mr. Marshall, October 11, 1905. The female exhibits a patch even larger than that of the male, and of a shape which approximates more closely to the model shown in Fig. 1.

2. *Planema poggei*, Dew., ♂, from Buddu, between Entebbe and the mouth of the Kageru River, west shore of Lake Victoria Nyanza; collected December 3, 1902—March 1, 1903, by T. T. Behrens, R.E. This *Acræine* butterfly with its broad fulvous band crossing the fore-wing, and white band crossing the hind-wing is evidently the primary model of the particular variety of the *semifulvescens*, Oberth., form of *A. johnstoni*, shown in Fig. 2a.

At the same time the latter exhibits a nearer approach to the *planemoides*, Trim., ♀ form of *Papilio dardanus*, Brown., one of its co-mimics (compare Plate XX, Fig. 4), than it bears to the central model of the group, *Planema poggei*.

- 2a. *Acræa johnstoni*, form *semifulvescens*, Oberth., ♀. From Taveta (about 2500 feet), British East Africa; May 15, 1905, Rev. K. St. Aubyn Rogers. This form possesses a pure white patch on the hind-wings, while the inner area of the fore-wings is black instead of fulvous as in typical *semifulvescens* (Plate XXI, Fig. 3a). This form appears to mimic the *planemoides* female of *Papilio dardanus* more closely than any other member of the large group clustered round *Planema poggei* (compare Plate X of the present volume, accompanying Mr. S. A. Neave's memoir).
3. *Planema latifasciata*, E. M. Sharpe, ♂; from Toro, W. Uganda (7-9000 ft.). November—December 1900: Major Rattray. This *Planema* is the model for the *toruna* form of *johnstoni* represented in the next figure.
- 3a. *Acræa johnstoni*, form *toruna*, H. Grose-Smith, ♂; from the same locality and date as the preceding. The mimetic likeness is strong in the deep rich brown of the inner area of the fore-wings and basal region of hind-wings in model and mimic, in the fulvous subapical band crossing the fore-wing and discal band crossing the hind-wing, and finally in the dark ground colour external to these striking markings.

In all forms of *Acræa johnstoni* here represented (Figs. 1a, 1b, 2a, and 3a), the under-side exposed during prolonged rest, when most of the fore-wing is hidden by

the hind, is not mimetic of the respective Danaine (Fig. 1) and Acræine (Figs. 2 and 3) models, but presents an appearance synaposematic with many *Acræas* of about the same size. During flight, on the other hand, and probably during brief rest, nearly the whole of the fore-wing under-side is revealed, and the effect is then such as to reinforce the mimetic resemblance of the upper-side.

SEPTEMBER 22nd, 1906.